

ANATOMY OF THE PERICARP OF CLIBADIUM,  
DESMANTHODIUM AND ICHTHYOTHERE  
(COMPOSITAE, HELIANTHEAE) AND  
SYSTEMATIC IMPLICATIONS

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ABSTRACT

The closely related genera, *Clibadium*, *Desmanthodium*, and *Ichthyothere* (Compositae, Heliantheae) are distributed in Mexico, Central America, and Northern and Central South America. Some of the species of *Clibadium* (e.g., *C. laxum*) have drupaceous achenes, which is unusual in the family. Comparative anatomical studies of fruits of the three genera show a strong similarity in the arrangement of the epidermis, hypodermis, and phytomelan and fiber layers. In most regards, *Desmanthodium* and *Ichthyothere* are more similar to each other than either is to *Clibadium*. The method of deposition of the phytomelan in all three genera begins with a series of tubes and cones from the fiber layer followed by patchy deposition of dark resistant material that eventually solidifies into a continuous layer. The phytomelan layer probably functions to protect the developing embryo and may also serve in regulating timing of germination.

The genus *Clibadium* L. of the Compositae (tribe Heliantheae), with 30–40 species ranging from Mexico to Peru, is unusual among members of the family in that some species have drupaceous achenes. Only two other genera of the family are known to have similar fleshy fruits (Huber, 1898; Norlindh, 1977): *Chrysanthemoides* Tourn. ex. Fabr. (tribe Calenduleae) and *Wulffia* Neck. ex Cass. (Heliantheae). Because *Clibadium* has already been studied for flavonoids (Bohm & Stuessy, 1981a), for sesquiterpene lactones and polyacetylenes (Czerson, et al., 1979), and for chromosome numbers and morphology for an eventual systematic synthesis by the senior author, an investigation of the anatomy of the unusual fruits of *Clibadium* would seem helpful. Especially useful would be indications of possible subgeneric groupings to test the sectional classification of Schulz (1912) and to compare with the broad flavonoid differences documented recently (Bohm & Stuessy, 1981a).

*Clibadium* is closely related to *Desmanthodium* Benth., which has eight species from Mexico and Central America, and to *Ichthyothere* Mart., with 15 species in South America, especially Brazil (Stuessy, 1977). Although the achenes of these other two genera are not known to be fleshy, a comparative examination of fruit anat-

omy would be useful to provide clues to evolutionary relationships both within and among all three taxa. This is especially important because the senior author (1977) has judged the three genera to be closely related (all placed in subtribe *Milleriinae*) whereas Robinson (1978, 1981) has recommended that each be placed in a separate subtribe (*Clibadiinae*, *Desmanthodiinae*, and *Melampodiinae*) of the *Heliantheae*. In addition, our preliminary studies on the pericarp of *Clibadium* provided some insights on the method of formation of the stony phytomelan layer. This dark brown or black layer is known to occur in the *Compositae*, primarily in the tribes *Eupatorieae* and *Heliantheae* (Hanausek, 1912; Vaughan, 1970; Misra, 1972; Wagenitz, 1976; Hegnauer, 1977). It was hoped that understanding the initiation and development of the phytomelan layer in the three genera, therefore, might provide even further insights to their evolutionary affinities as well as help reveal the mode of deposition of the phytomelan layer itself. A number of studies have been done on the origin of this layer in the *Compositae* (Hanausek, 1902, 1907, 1912; Vries, 1948; Politis, 1957; Misra, 1964, 1972; Pullaiah, 1979, 1981), but they have been inconclusive as to events that result in its formation.

The purposes of this paper, therefore, are to: (1) examine the achenial anatomy of different species within *Clibadium*, *Desmanthodium*, and *Ichthyothere* to learn if subgeneric groupings might be suggested within each; (2) postulate evolutionary relationships among the three genera based on pericarp anatomy; and (3) gain some insights on the development of the phytomelan layer in all three genera.

#### MATERIALS AND METHODS

Nineteen species of *Clibadium* (38 populations), three of *Desmanthodium* (five populations) and eight of *Ichthyothere* (11 populations) were examined (Table 1). Preparation of the achenes for studying the outer surface of the phytomelan layer was accomplished by soaking in 10% NaOH for 4–14 hours followed by mechanical removal of the outer pericarp and finally by washing in distilled water. A few preparations were soaked in dilute HCl for one hour and then washed. This surface was then shadow-coated with gold and viewed in the SEM.

Table 1. Voucher specimens of taxa of *Clibadium*, *Desmanthodium*, and *Ichthyothere* examined by SEM for external surface of the phytomelan layer and by light microscopy for pericarp anatomy. All vouchers cited here and elsewhere in this paper are at OS unless indicated otherwise (herbarium acronyms in parentheses after Holmgren, Keuken, and Schofield, 1981).

SF = Stuessy & Funk; SG = Stuessy & Gardner; SJ = Stuessy & Jansen; SN = Stuessy & Nesom.

F = freehand sections; P = paraffin-embedded sections; SEM = external SEM observations; ss = serial sections.

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Taxa and Vouchers

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**Clibadium** *anceps* Greenm., SG 4518 [P,SS], Wilbur & Stone 10678 [SEM]; *C. arbo-reum* J.D. Smith, Dwyer 11415 [SEM], SG 4574 [F, SEM]; *C. asperum* (Aubl.) DC., Castañeda 6144 (NY) [SEM], Killip & Smith 26834 (GH) [SEM], McDaniel 2366 (US) [SEM], SN 5899 [SEM]; *C. glomeratum* Greenm., SG 4517 [SEM, SS]; *C. grandifolium* S.F. Blake, Gentry 3034 [SEM], SG 4533 [P,SS]; *C. laxum* S.F. Blake, SJ 4942 [P, SEM, SS]; *C. leiocarpum* Steetz in Seem., Almeda & Nakai 10678 [SEM], SG 4456 [F]; *C. micranthum* O.E.Schulz, Killip & Smith 24822 (NY) [SEM]; *C. parviceps* S.F. Blake, Williams 10478 (US) [SEM]; *C. pentaneuron* S.F. Blake, Peláez 510 (US) [SEM] SF 5709 [SS]; *C. peruvianum* Poepp. ex DC., Killip & Smith 27263 (US) [SEM], Mexia 6506a (NY) [SEM]; *C. pilonicum* Stuessy, Hartman 3963 [SEM]; *C. pittieri* Greenm., Cuatrecasas 13709 (US) [SEM], Forero & Gentry 725 (COL) [SEM], Standley 45815 (US) [SEM], SG 4465 [SS]; *C. psilogynum* S.F. Blake, Weberbauer 7864 (GH) [SEM]; *C. sessile* S.F. Blake, Hartman 3916 [SEM]; *C. sprucei* S.F. Blake, SN 4811 [SS]; *C. surinamense* L., Bristor 690 (US) [SEM], Cuatrecasas 14004 (US) [SEM], SG 4451 [SEM], SN 5856 [SS], SPJ 4935 [SEM]; *C. terebinthinaceum* DC., Cuatrecasas 23932 (F) [SEM], Fuchs et al. 21728 (COL) [SEM], SF 5737 [F]; *C. trianae* S.F. Blake, Cuatrecasas 6475 (F) [SEM], SN 4680 [F].

**Desmanthodium** *fruticosum* Greenm., King & Soderstrom 505 (UC) [SEM], SG 4115 [P, SEM, SS]; *D. hondurensis* A. Molina, Hazlett 849 (MO) [SEM], SG 4390 [SS]; *D. perfoliatum* Benth., SG 4306 [F, SEM].

**Ichthyothere** *agrestis* Baker in Mart., Hatschbach 19911 (F) [F]; *I. cordata* Malme, Maguire & Maguire 44510 (NY) [F]; *I. cunabi* Mart. in Buchn., Dusén s.n. (MO) [F]; *I. hirsuta*, Irwin et al. 25876; (MO) [SS]; *I. latifolia* Gardn., Irwin et al. 34716 (MO) [F]; *I. rufa* Gardn., Argent 6711 (NY) [SEM]; *I. scandens* S.F. Blake, Cuatrecasas 13313. (COL) [F]; *I. terminalis* (Spreng.) Malme, Assis 157 (UC) [SS], Forero, Bastidas & Ramírez 882 (NY) [P, SS], Pereira 7535 (NY) [P, SEM, SS], Prance 8603 (NY) [SEM].

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Sections of pericarp were made free-hand and by traditional paraffin embedding and sectioning (Sass, 1958). Stains used for the paraffin mounts were safranin and fast green. The serial sections were done in all paraffin material plus 12 other collections (Table 1) cut free-hand to determine the degree of constancy of pericarp anatomy throughout the achene.

## RESULTS

### Structure of Pericarp

The anatomy of the pericarp in *Clibadium*, *Desmanthodium*, and *Ichthyothere* is basically similar with five distinct zones observable (Fig. 1–6): epidermis, hypodermis, phytomelan layer, fiber zone, and internal parenchyma. Within each genus a constancy of anatomical features exists among the species examined. In addition, the organization of the pericarp is constant throughout the entire length of the achene. Slight variations occur in numbers of hypodermal cell layers and thickness of the phytomelan layer, but they are minor and do not obscure nor contradict patterns observed and documented (Figs. 1–6; Table 2).

The pericarp is the thickest in *Clibadium*, with *Ichthyothere* next, followed by *Desmanthodium*. The species of *Clibadium* with drupaceous fruits (such as *C. laxum*) are such due to an inflated hypodermis with more and larger cells and cell layers. In all other respects they have the same structure as the other species of the genus with dry achenes. The epidermis and internal parenchyma provide no significant taxonomic characters for differentiating the three genera. The hypodermis, however, does differ, with parenchyma being 2–5 cells thick and radially arranged in *Clibadium* and 3–6 cells thick and irregularly arranged in *Ichthyothere*. *Desmanthodium* has only 1–2 parenchyma cell layers. The phytomelan layer is different in the three genera (Figs. 1–3; Table 2), and this is

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Figures 1–6. Transections of mature (Fig. 1–3) and immature (4–6) pericarps of *Clibadium*, *Desmanthodium*, and *Ichthyothere*. 1. *C. laxum*, SJ 4942. 2. *D. fruticosum*, SG 4115. 3. *I. terminalis*, Pereira 7535 (NY). E, epidermis; H, hypodermis; P, phytomelan layer; F, fiber zone; IP, internal parenchyma.

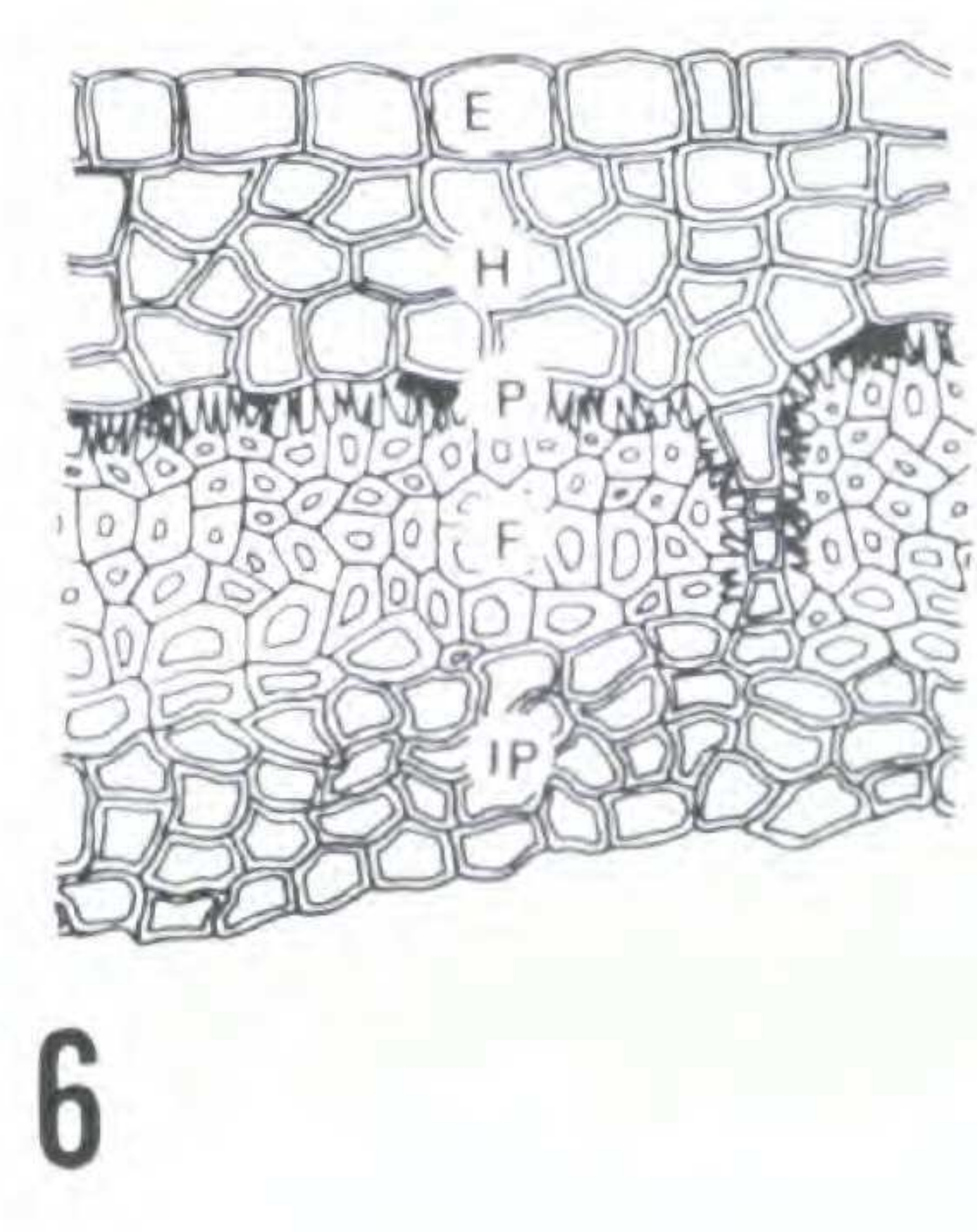
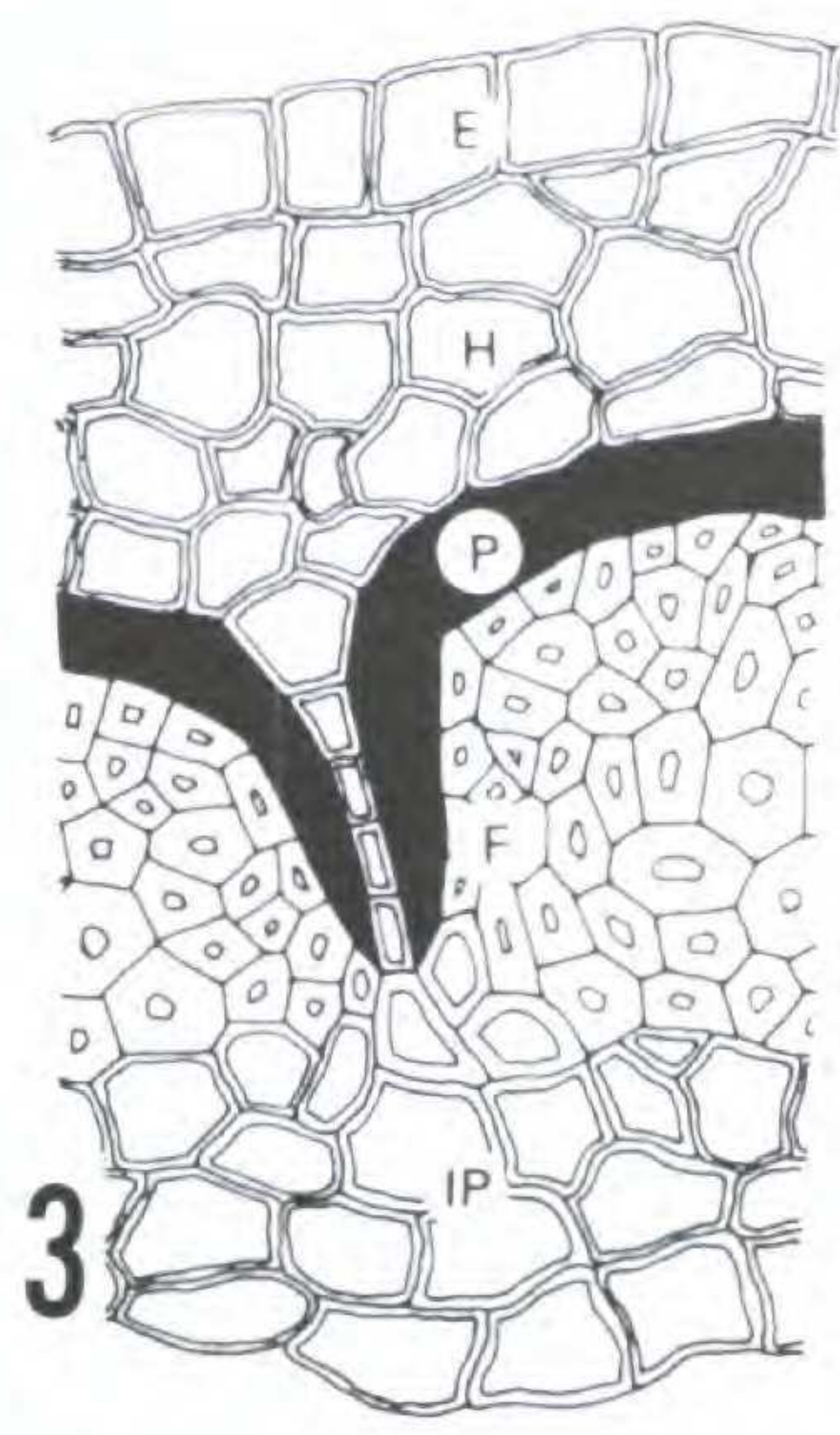
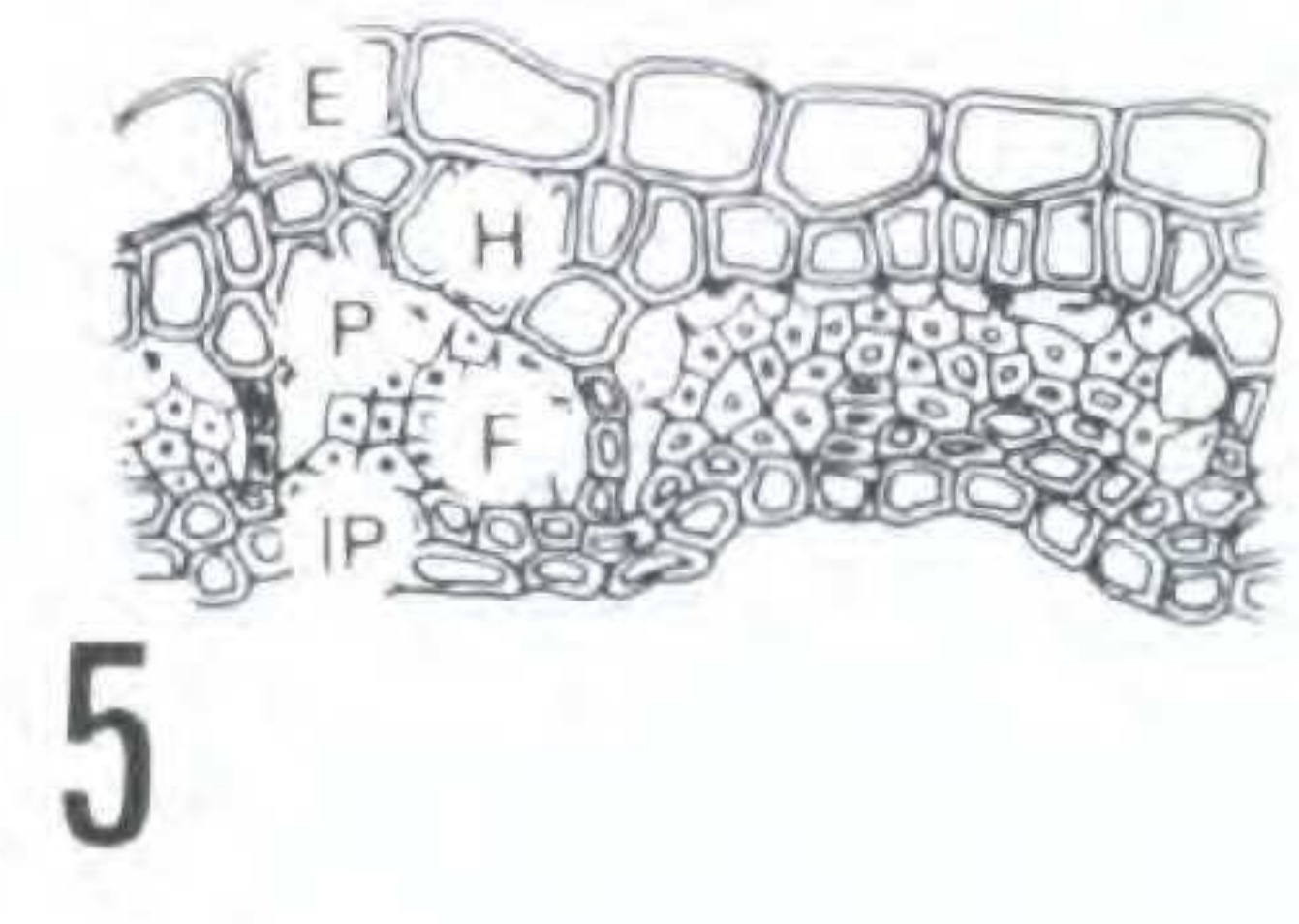
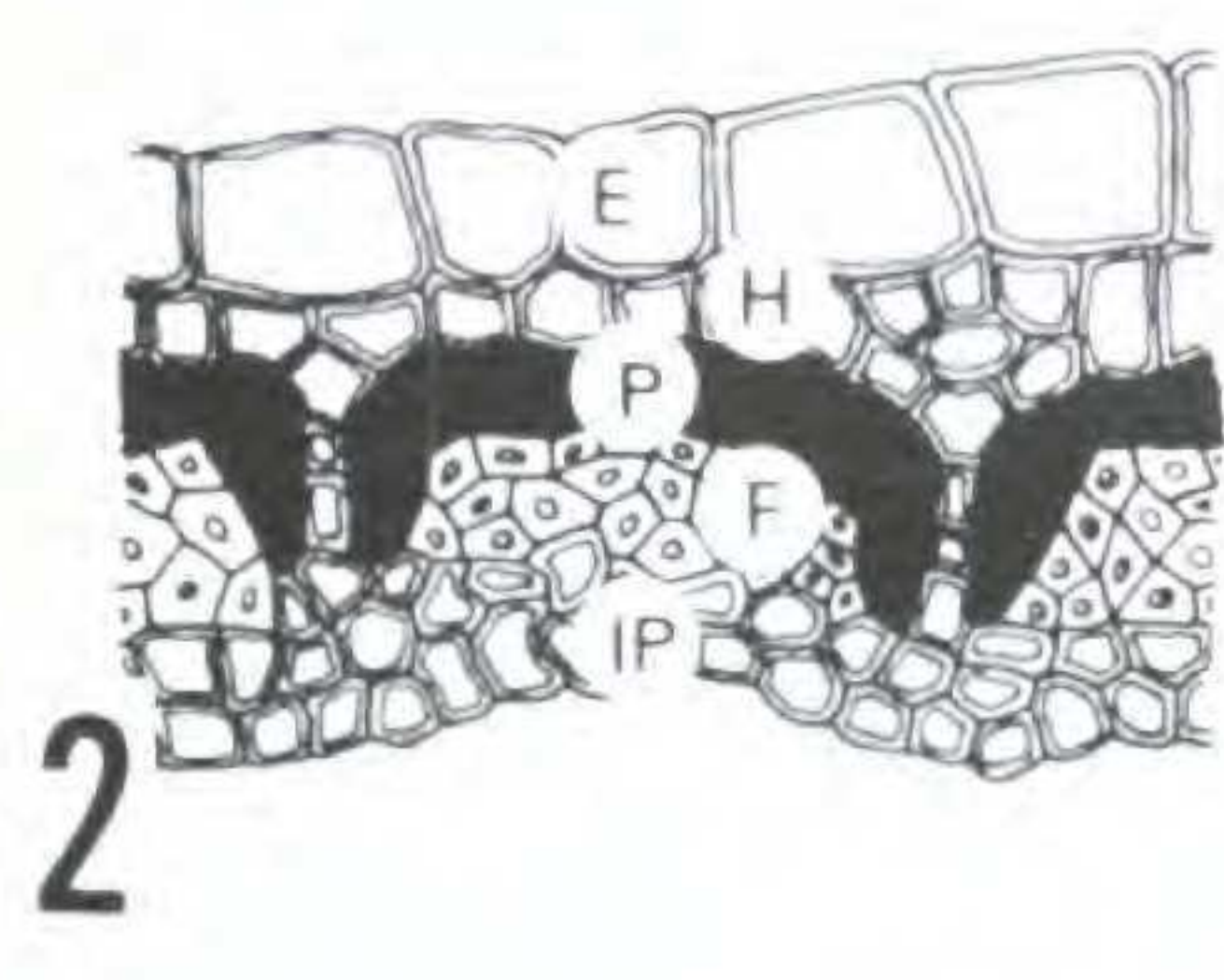
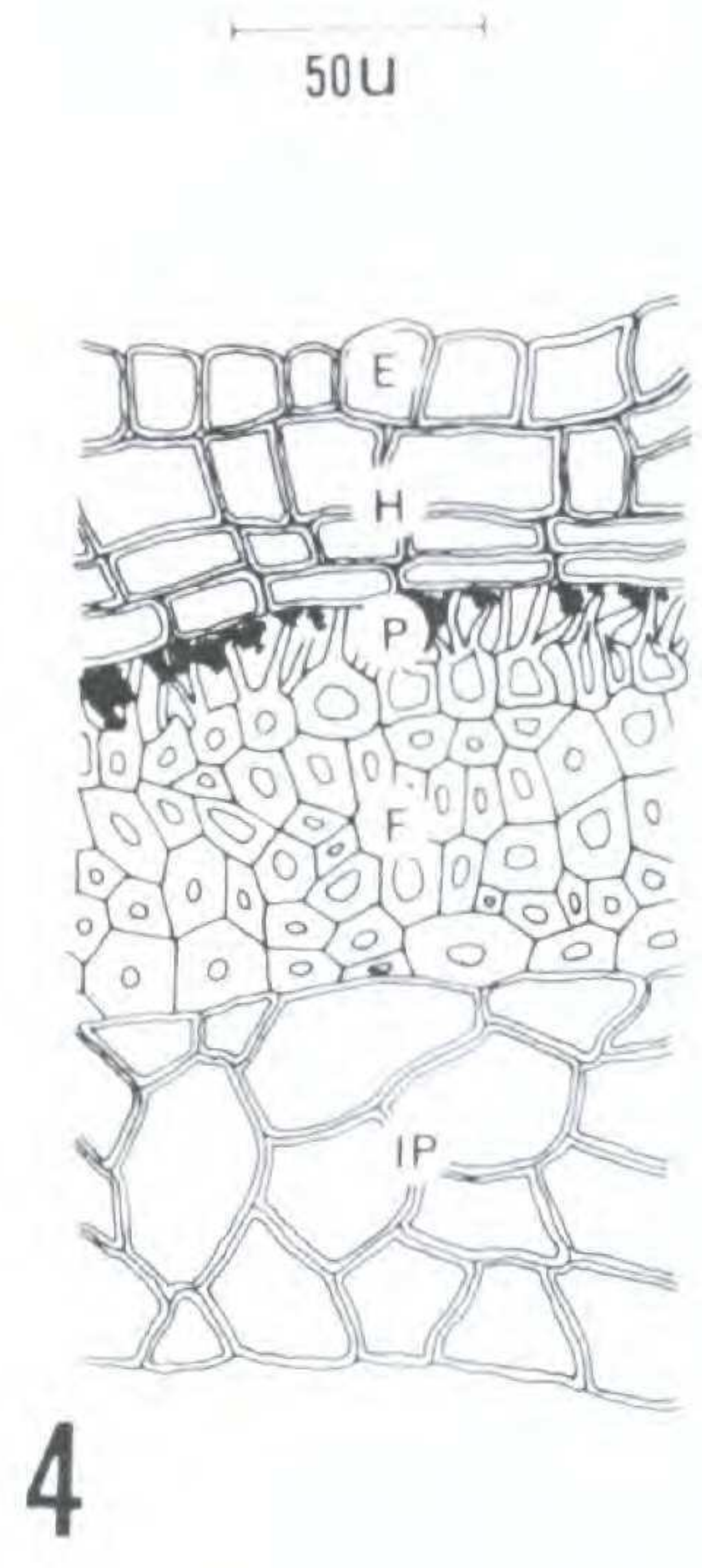
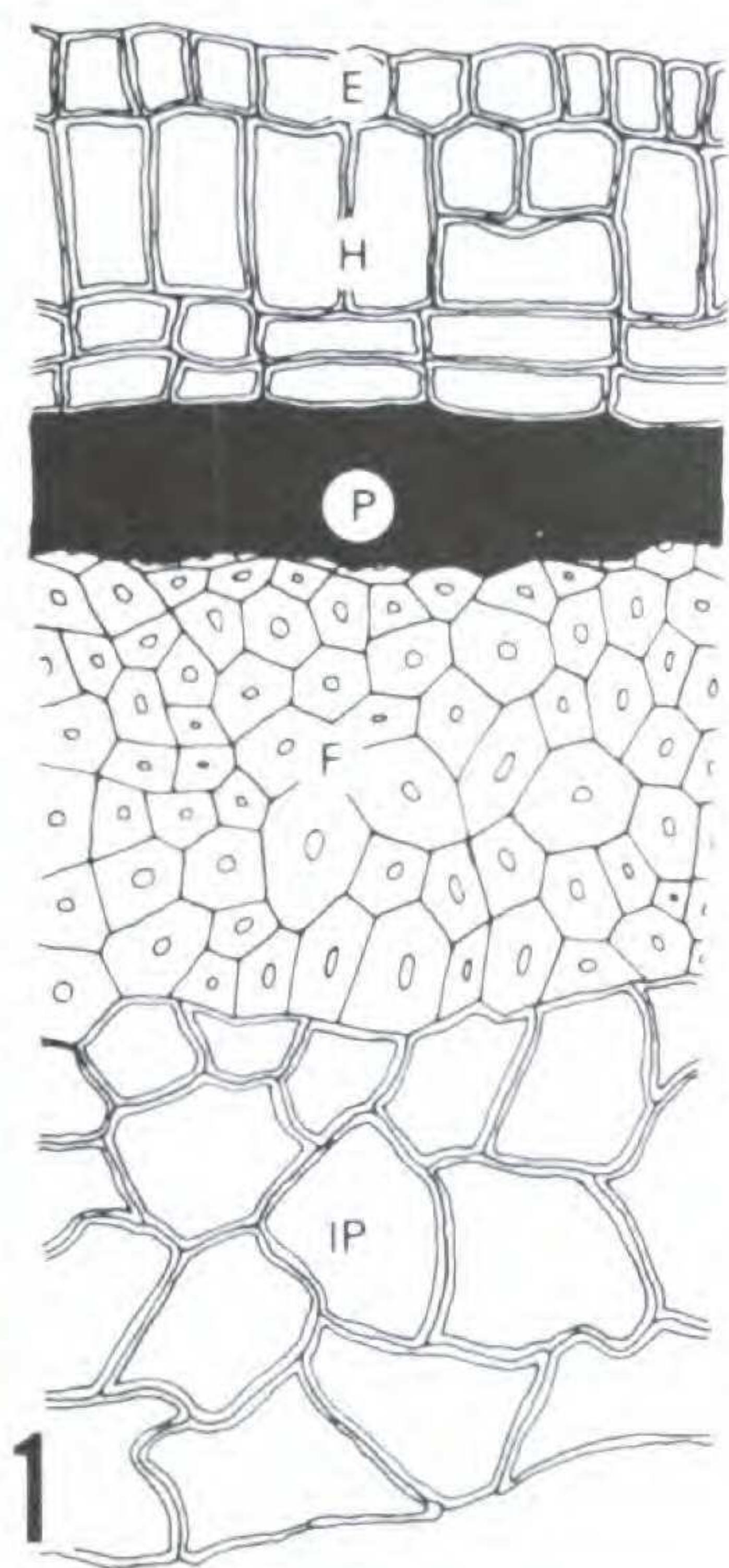


Table 2. Comparison of pericarp anatomy in *Clibadium*, *Desmanthodium*, and *Ichthyothere*.

Region of pericarp	<i>Clibadium</i>	<i>Desmanthodium</i>	<i>Ichthyothere</i>
Hypodermis	2-5 cell layers of parenchyma in radial files	1-2 cell layers of parenchyma	3-6 cell layers of parenchyma irregularly arranged
Phytomelan layer	continuous and regular	discontinuous, associated with fiber bundles	discontinuous, associated with fiber bundles
Fiber zone	continuous, 4-10 cell layers thick	discontinuous, bundles of 15-55 fibers	discontinuous, with large (70-140) and small (20-40) bundles of fibers

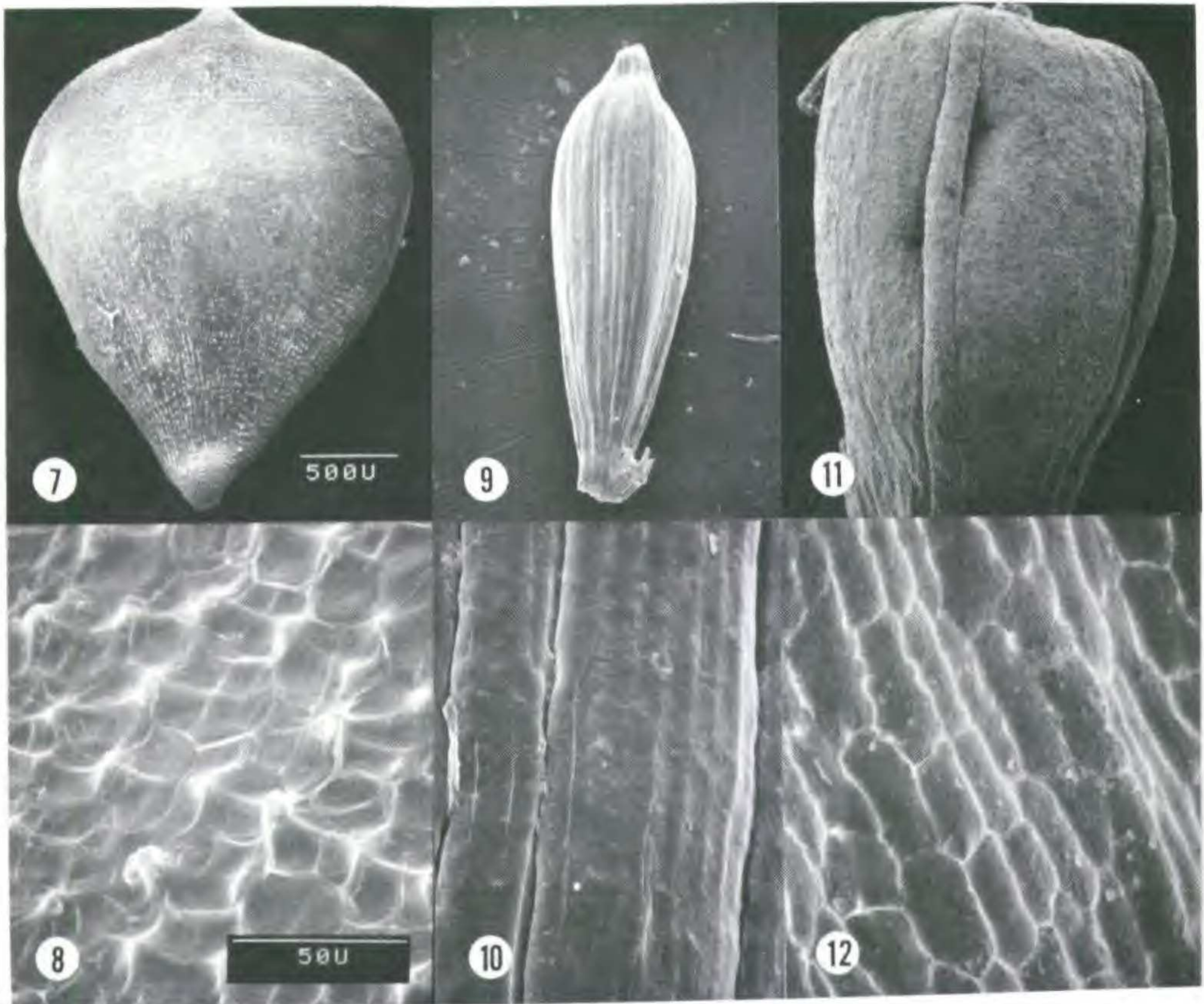
especially evident in surface configuration (Figs. 7–12). *Clibadium* has a thick continuous phytomelan layer, *Ichthyothere* has the layer interrupted by eight longitudinal grooves, and *Desmanthodium* has numerous longitudinal grooves over the entire surface of the achene. In all taxa the phytomelan is intimately associated with the fiber zone immediately below. The fibers appear similar in the three genera, but in *Clibadium* they form a continuous layer (as with the phytomelan), in *Ichthyothere* the fibers are interrupted eight times, and in *Desmanthodium* they are interrupted many times resulting in numerous small clusters.

### Variations in Upper Surface of Phytomelan Layer

The upper surface of the phytomelan in *Clibadium*, *Desmanthodium*, and *Ichthyothere* differs at the generic level with *Desmanthodium* being nearly smooth and the former and the latter having more regular cellular sculpturing (Figs. 7–12). These cellular patterns result from the formation of phytomelan against the cells of the hypodermis; the phytomelan itself is acellular. Within each genus, minor variations of sculpturing exist, but they are not significant for the recognition of most species and they also show some developmental variation.

### Development of Phytomelan Layer

Examination of cross-sections of young achenes of species of *Clibadium*, *Desmanthodium*, and *Ichthyothere* (Figs. 4–6) reveals general aspects of the system of development of the phytomelan layer. In all three genera the fiber zone below and hypodermis above serve as templates between which the phytomelan begins to be deposited. A developmental sequence in *Clibadium surinamense* serves as an example for these details (Figs. 13–18). The upper cell layer of the fiber zone has tubular or cone-shaped extensions (Figs. 4 & 13), which touch the hypodermis. It is not clear whether the phytomelan derives from the fiber zone, the hypodermis, or both. The phytomelan thickens and fuses laterally (Figs. 14–16), and eventually forms a hardened solid layer (Figs. 17 & 18). *Ichthyothere* and *Desmanthodium* develop in a similar fashion (Figs. 5, 6, 19, & 20 for similar early stages).



Figures 7–12. External surface of phytomelan layer of mature achenes of *Clibadium*, *Desmanthodium*, and *Ichthyothere*. 7 & 8. *C. pittieri*, Standley 45815 (US). 9 & 10. *D. fruticosum*, King & Soderstrom 5058 (UC). 11 & 12. *I. rufa*, Argent 6711 (NY). All scale as in Figs. 7 & 8.

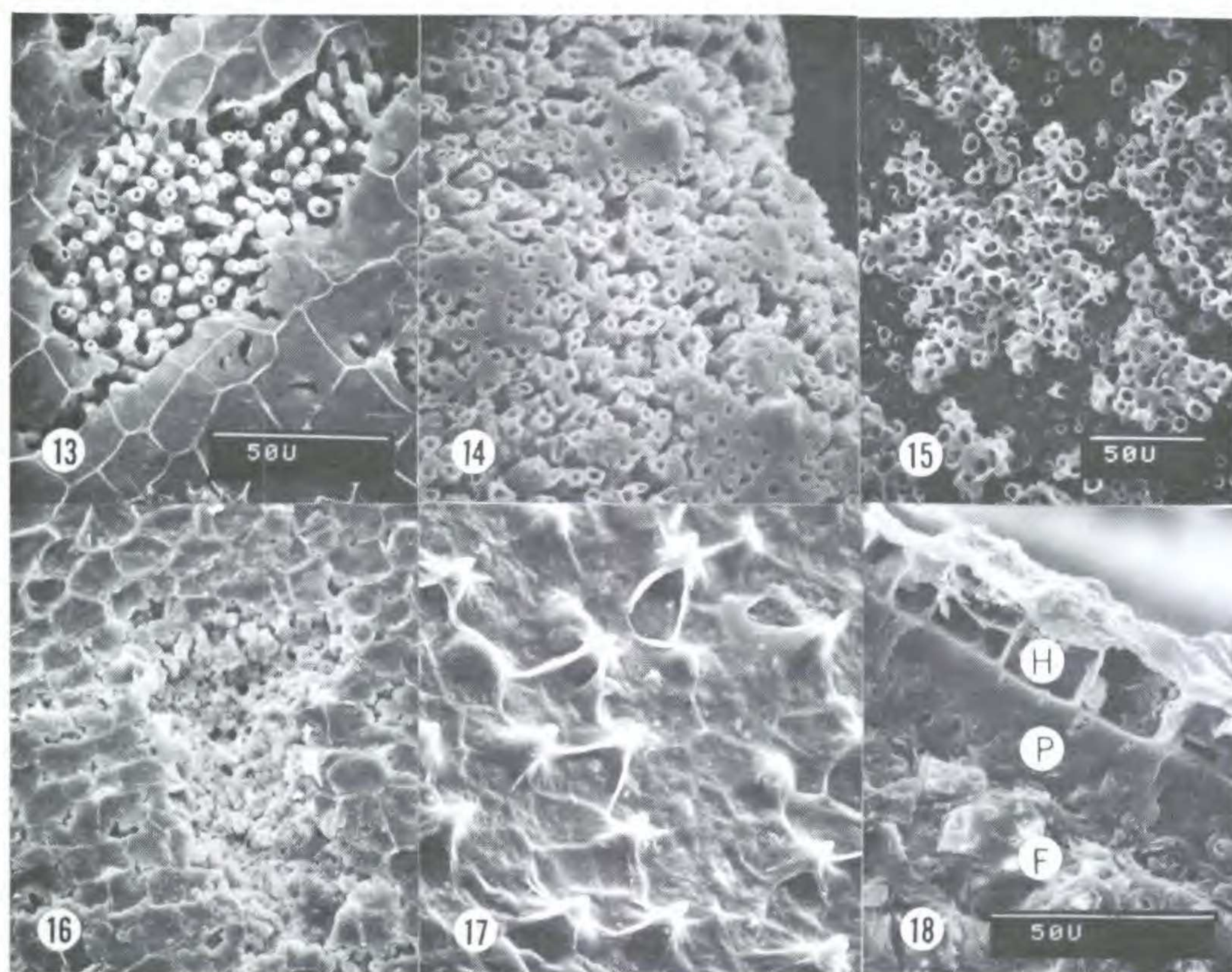
#### DISCUSSION

##### **Systematic and Evolutionary Significance of Variations in Pericarp Structure**

Because of the initial interest in the unusual drupaceous achenes of some species of *Clibadium*, it was hoped that many differences in pericarp structure would be found *among* species of the genus. Although some minor variations do occur (e.g., a more elevated series of tubercles on the upper surface of the phytomelan layer in *C. sychnocephalum*), they are not generally useful at either the specific or subgeneric levels within any of the genera.

The differences in pericarp structure among the three genera, however, are significant and help distinguish them more clearly (cf. differences listed in Table 2). A more important question is how



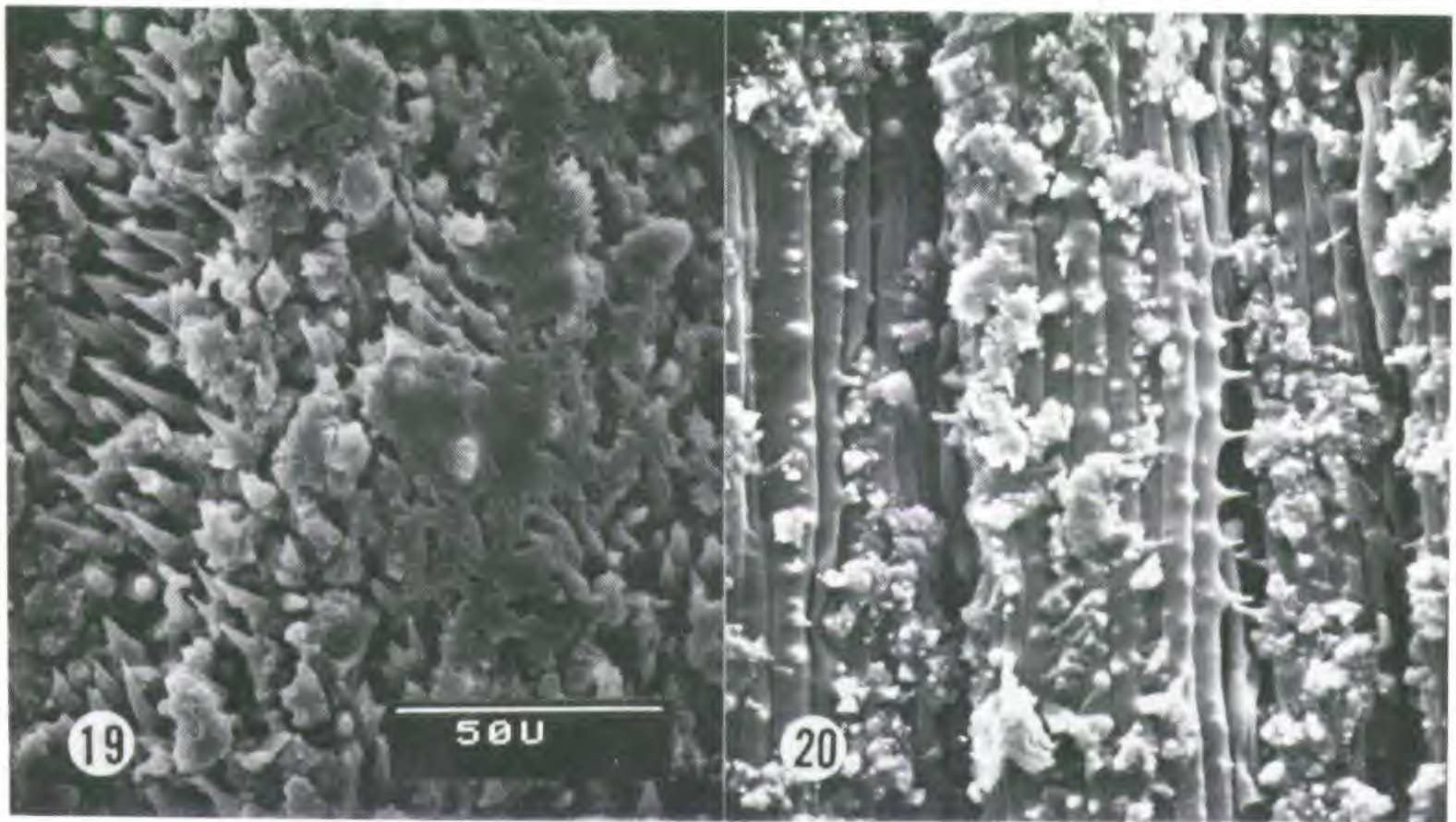


Figures 13–18. Development of phytomelan layer in *Clibadium surinamense*. **13.** Surface of very immature achene with hypodermis partially removed, showing tubular extensions of fibers (FAA preservation). **14.** Surface of young achene with hypodermis completely removed showing initiation of phytomelan around tips of extensions (FAA preservation. NaOH cleaning). **15.** Inner view of hypodermis showing attachment of upper part of extensions with beginnings of envelopment by phytomelan and extensions fractured below (dry). **16.** Surface of nearly complete and phytomelan layer (dry). **17.** Surface of mature phytomelan layer (dry, with NaOH cleaning). **18.** Transection of mature achene wall (dry) with solid phytomelan layer (P) between hypodermis (H) and fibers (F) below; compare with Fig. 1. Figs. 13, 15, 16, 18, *Stuessy & Gardner 4451*; 14, *Stuessy et al, 4935*; 17, *Bristor 690 (US)*. Figs. 13, 14, & 17, and 15 & 16 same scales, respectively.

closely related the three genera are to each other. The structure and development of the pericarp is essentially the same and suggests a strong evolutionary tie. Particularly noteworthy are the extensions of the fibers around which the phytomelan accumulates. Although a number of Compositae have been analyzed for pericarp features (Hanausek, 1902, 1912; Briquet, 1916; Giroux, 1930, 1933; Vries, 1948; Misra, 1964, 1972; Carlquist, 1958; Dittrich, 1968a, b, 1969), it remains to be seen how relatively close *Clibadium*, *Desmantho-*

*dium*, and *Ichthyothere* will be after many other genera of the Heliantheae are investigated. Nonetheless, the similarity of pericarp features does not appear to support Robinson's (1978, 1981) placement of *Clibadium*, *Desmanthodium*, and *Ichthyothere* in separate subtribes.

The strong similarities of pericarp structure in *Clibadium*, *Desmanthodium*, and *Ichthyothere* make it difficult to determine the relationships of the genera one to another. The most significant point seems to be that *Desmanthodium* and *Ichthyothere* are similar in having discontinuous phytomelan as opposed to it being continuous in *Clibadium*. This suggests that the two are more closely related than either is to *Clibadium*. On the other hand, the similar cellular patterns of the external phytomelan surface in *Clibadium* and *Ichthyothere* argue for their close relationship, in contrast to the smooth surface in *Desmanthodium*. The ontogeny of the phytomelan layer in all three genera is essentially the same, except that *Desmanthodium* and *Ichthyothere* have more conical and smaller fiber extensions whereas those in *Clibadium* are larger and more tubular.



Figures 19 & 20. Surface of young achene showing patchy development of phytomelan layer in *Ichthyothere terminalis* (19, dry, NaOH cleaning; Prance et al. 8603, NY) and *Desmanthodium perfoliatum* (20, FAA, HCl cleaning, Stuessy & Gardner 4306). Same scale.

Studies on the structure and development of the pericarp do not indicate which type is the most evolutionary primitive and which is more advanced. Because of the absence of comprehensive studies on genera of the Heliantheae, the basic pattern in the tribe is not yet known. This makes evolutionary directionality difficult to determine. One might speculate that the structure of *Clibadium* may be more primitive simply because it is a more simple pattern. Chromosome numbers give limited support to this idea because *Clibadium* is known as  $n = 16$  and  $24$  ( $x =$  probably  $8$ ) (Turner & King, 1964; Coleman, 1968; Powell & King, 1969a, b; Powell & Cuatrecasas, 1970; Grashoff, Bierner, & Northington, 1972; Solbrig, et al., 1972), *Desmanthodium* as  $n = 18$  (Fay, 1974; Keil & Stuessy, 1977), and *Ichthyothere* as  $n = 32$  (Coleman, 1970). An ancestral base of  $x = 8$  for the entire complex is the simplest explanation for these data which would make *Clibadium* and *Desmanthodium*, as the lowest level polyploids, more primitive than the others (*Desmanthodium* may have arisen by polyploidy from an  $x = 9$  ascending aneuploid line). The flavonoid data give some suggestion that *Clibadium* has a more primitive biochemical profile than *Desmanthodium*, in that the latter accumulates more mono-, di-, and tri-methyl derivatives (Bohm & Stuessy, 1981b). Alternatively, however, the pattern of phytomelan interrupted by parenchymal rays as in *Desmanthodium* and *Ichthyothere* might be more primitive because this aspect also occurs (Hanausek, 1912; Vries, 1948; Vaughan, 1970) in *Guizotia abyssinica*, *Helianthus annuus*, *Madia sativa*, *Rudbeckia fulgida*, and *Sclerocarpus uniserialis*, taxa of the same tribe (Heliantheae). A continuous layer, however, is also known (Hanausek, 1912) in *Eclipta alba*, *Engelmannia pinnatifida*, *Silphium trifoliatum*, and *Verbesina encelioides* of the Heliantheae. More data are obviously needed from many other genera.

#### Development of Phytomelan Layer

A number of studies on the development of phytomelan in the Compositae exist (e.g., Hanausek, 1902, 1912; Vries, 1948; Politis, 1947; Misra, 1964, 1972; Pullaiah, 1979, 1981). These and our own studies have reported the following observations: (1) the phytomelan forms between the hypodermis and the fiber zone; and (2) the phytomelan is non-cellular, very resistant, and whatever markings or sculpturing it has derives from the hypodermal cell layer in

contact with it (e.g., the tubercles on the phytomelan surface of *Clibadium pittieri* reflect depressions at cell wall junctures of the hypodermis, Figs. 7 & 8). Previous workers (Vries, 1948; Misra, 1964, 1972; Pullaiah, 1979, 1981) have believed the phytomelan to be derived from exudates from the hypodermis. This may be so, but it could not be determined to our satisfaction. Alternatively, material may be exuded from the fiber zone or from both sides of the location of deposition. Detailed cytological and histochemical studies will be needed to resolve this question. The tubes and cones in *Clibadium*, *Desmanthodium*, and *Ichthyothere* may function simply as a framework around and within which the phytomelan solidifies, but they also may transport materials to the site of deposition (this seems especially possible in *Clibadium* with the numerous tubes, more than one would think necessary for just structural purposes; see Fig. 13).

The chemical nature of phytomelan is still unknown although it has been proposed by Dafert and Miklausz (1912) to have a molecular formula  $x(C_6H_{10}O_5)-yH_2O$  and suggested by Hegnauer (1964, 1977) to be a polyacetylene. Our studies show that it is not modified by dilute NaOH or HCl treatment, whereas the cells of the epidermis and hypodermis are easily softened and destroyed.

Likewise, the adaptive value of the phytomelan layer is uncertain, but it probably functions as a protective device for the mature fruit and may also regulate the timing of seed germination. The fact that this layer is found principally within the tribes Eupatorieae and Heliantheae (Hanausek, 1912; Misra, 1972) also gives it special taxonomic potential at the higher levels of the hierarchy in the family. The homologies of structure and developmental patterns will have to be determined before their full efficacy can be appreciated.

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